THE EFFECT OF PARENTING STYLES AND BIPARENTAL COOPERATION ON REPRODUCTIVE SUCCESS IN THE CAROLINA CHICKADEE (*POECILE CAROLINENSIS*)

A thesis presented to the faculty of the Graduate School of Western Carolina University in partial fulfillment of the requirements for the degree of Master of Science in Biology.

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ABSTRACT

THE EFFECT OF PARENTING STYLES AND BIPARENTAL COOPERATION ON REPRODUCTIVE SUCCESS IN THE CAROLINA CHICKADEE (*POECILE CAROLINENSIS*)

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Socially monogamous birds use biparental care to off-set the high cost of energy, resources, and time needed to successfully rear their offspring. To be effective, biparental care requires cooperation between the parents. While parental effort and task allocation have been well studied in birds, less research has focused on how cooperation between parents affects their reproductive success. In this study, I investigated between-individual differences in parental behavior (i.e. parenting styles) and how parenting styles influence strategies of cooperation in Carolina Chickadees. I examined individual effort towards provisioning and nest defense to understand the variation in parenting styles among chickadee parents. I measured provisioning effort as visits per hour per chick during 8-hour observational periods using a video camera at the nest. I measured nest defense effort as the distance (m) from predator during 7-minute trials using a taxidermic predator near the nest. I estimated similarity between the parents using z-scores of parental behavior and I measured reproductive success as chick growth per day, fledgling mass, and number of chicks fledged. I found a statistically significant positive correlation in effort

between provisioning and nest defense in individuals, so the degree of parental contribution was consistent across tasks. Further, I found that when male effort matched or exceeded female effort, pairs produced larger chicks at fledging. Thus, the degree of parental contribution provided by the male chickadee in a pair impacts chick quality. The results of this study suggest that male parental contribution in Carolina Chickadees is critical when parents are dissimilar in their parental effort.

INTRODUCTION

Biparental care is a derived strategy of parental care common among vertebrate taxa (Burley and Johnson 2002, Caldwell and de Oliveira 1999, DeWoody et al. 2000, Gubernick and Alberts 1987) especially birds (Cockburn 2006), but also found in some invertebrate taxa (Creighton et al. 2015, Suzuki 2013). Theoretical and empirical studies suggest that biparental care evolved as a mechanism to reduce costs to females when young are dependent and parental investment is high and to reduce costs to males from lost paternity when females are promiscuous and choosy (Westneat and Sherman 1993; Burley and Johnson 2002; Suzuki 2013). While biparental care may be adaptive, parents can mediate biparental care to maximize success using flexible behavioral strategies to compensate for changing conditions in the environment, themselves or their partners. Parents can minimize time and energy costs by distributing the burden of care between parents to maximize lifetime reproductive success (Balshine-Earn 1997, Kavelaars et al. 2019, Santos and Nakagawa 2012). Thus, parents should maximize the benefits, relative to the energetic costs, by cooperating. However, parents typically have competing interests and may benefit by shifting more of the burden of care to their partner (Trivers 1972). How parents navigate the conflict of interest during cooperative parenting remains unclear (e.g. Harrison et al. 2009, Kavelaars et al. 2019, Kokko 1999). In this study, I investigated how parental effort in individuals influence cooperative strategies of biparental care in birds.

If biparental care in birds is necessary to raise high quality young, then parents should cooperate to get the highest possible fitness. But, individual effort during cooperation may be influenced by many intrinsic and extrinsic factors leading to variation in strategies among individuals and within pairs (Clutton-Brock 1991, Smiseth et al. 2012). Successfully rearing

young in altricial birds requires investment in nest building, incubation, brooding, provisioning, and nest defense (Collias and Collias 1964, Nealen and Breitwisch 1997, Neudorf et al. 2013, Sanz and Moreno 1995, Walters et al. 2016). Parental tasks are often allocated by sex (Buitron 1988, Dawson and Bortolotti 2008) where females usually but not always (e.g. Collias and Collias 1964, Fraser et al. 2002) invest more heavily than males during early stages such as building the nest, incubating the eggs, and brooding the nestlings (Mendenhall 1979, Tomás et al. 2006, Walters et al. 2016). Other tasks, such as provisioning and nest defense, are typically shared between parents (Filliater and Breitwisch 1997, Redmond et al. 2009, Stodola et al. 2009). In shared tasks, conflicts can arise between the parents on how much effort each should provide because individual parents benefit if more of the burden of care is shifted to their partner (Trivers 1972). Increased effort towards parental care is costly; it leads to greater weight loss (Royle et al. 2002) and lowers adult survival (Griggio et al. 2009). Thus, paired cooperative parents rarely invest as heavily in shared tasks than they would as the sole provider in a uniparental system (Balshine-Earn 1997, Royle et al. 2002). However, cooperation to ensure an adequate level of care is given to the chicks might be difficult in shared tasks if parents cannot predict the strategy and investment level their partner is willing to provide. So, a possible resolution to this conflict of interest is innate stable individual effort towards parental tasks.

Stable individual effort towards parental tasks could create the conditions necessary for cooperation in biparental care. Cooperation in the shared tasks of biparental care can occur via the 'sealed bid' model of cooperation (Houston and Davies 1985). The "sealed bid" model states that individuals should commit to a certain level of parental care per breeding attempt based on factors such as brood size and quality, individual quality, or prey abundance, but not influenced by their partner's investment level. Using the 'sealed bid' is ideal for species that have reliable

indicators of parental competence beforehand (Schwagmeyer and Mock 2003) such as plumage color (Jawor and Breitwisch 2004) during courtship. Support for the 'sealed bid' model has been found in House Sparrows (*Passer domesticus*) (Schwagmeyer et al. 2002), Yellow Warblers (*Dendroica petechia*) (Lozano and Lemon 1996), Great Tits (*Parus major*) (Sanz et al. 2000), and Pied Flycatchers (*Ficedula hypoleuca*) (Slagsvold and Lifjeld 1988). Stability in parental investment behaviors by parents could provide a mechanism for the development of parenting styles where individuals have consistent and persistent approaches to caring for offspring (MacColl and Hatchwell 2003, Maestripieri 2001, Pittet et al. 2013, Wischhoff et al. 2018). By allocating effort consistently across time and persistently across contexts (i.e. having parenting styles), parents may be better able to cooperate between shared tasks because each parent has a sense of the level of effort their partner is willing to provide throughout the reproductive attempt.

Parenting styles could be influenced by intrinsic factors such as the physical condition of the parents. Parents in better condition should have parenting styles where they maintain higher levels of effort across multiple tasks over parents in poor condition. Therefore, if the physical condition of the parents influences parenting styles, then there should be a positive correlation between parental tasks among individuals (Kopisch et al. 2005, Wetzel and Westneat 2014). Extrinsic factors such as optimal habitat, weather conditions, and prey abundance can also affect the performance level of the parents (Dawson and Bortolotti 2000, Ens et al. 1992, Hakkarainen et al. 1997). That is, parents raising chicks in optimal habitat with an abundance of prey under favorable weather conditions will perform better than parents raising young in poorer conditions. Ultimately, intrinsic and extrinsic factors will influence brood quality that will reinforce positive correlations between parental tasks. Parents that feed chicks at a higher rate may be more willing to increase their effort towards nest defense because the reproductive value of the brood is

greater with the increased provisioning compared to parents that feed chicks less frequently (Griggio et al. 2009, Rytkönen 2002). Thus, if parent condition, brood quality, or the environment influences parenting styles, then parenting styles should exhibit positive correlations in effort between tasks within individuals. Conversely, life-history theory predicts that finite levels of time and energy could result in trade-offs between parental tasks (Stearns 1989). Thus, individuals may have parenting styles where they allocate more effort towards one task at the expense of another, which will result in a negative correlation in effort. White-rumped Swallow parents (*Tachycineta leucorrhoa*) displayed a trade-off in provisioning and nest defense where birds that defended more also fed the brood less often (Wischhoff et al. 2018). If parenting styles are most influenced by trade-offs, then parenting styles should exhibit negative correlations in effort between tasks within individuals.

Parenting styles, whether effort allocation positively co-varies or exhibits trade-offs in individuals, should dictate the optimal strategies used by parents to cooperate when raising young. The strategy that is most effective will depend on how individuals allocate their effort towards parental tasks. If trade-offs are evident and individuals exhibit parenting styles with negative correlations in effort between behaviors, then parents with dissimilar parenting styles should cooperate more effectively and have the highest reproductive success. This division-of-labor approach in cooperation should allow for an adequate expenditure of effort towards all parental tasks within a breeding pair where one parent will focus their effort towards one task, such as provisioning, and the other parent will focus their effort on another task, such as nest defense (Bartlett et al. 2005, Lombardo 1991, Zaias and Breitwisch 1989). If individuals exhibit parenting styles with positive correlations in effort between behaviors, then parents should assort by similarity where both parents contribute equally in all tasks. Positive assortative mating

occurs when similar birds pair up more frequently than expected by chance. Birds can assort positively by physical characteristics, such as plumage color (Cooke et al. 1976, Jawor et al. 2003) or by behavioral characteristics, such as temperament or equal contributions towards various parental tasks (Both et al. 2005, David et al. 2015, Harris and Siefferman 2014, Mariette and Griffith 2012, Nealen and Breitwisch 1997, Spoon et al. 2006). Additionally, pairs with highly similar parents tend to be more reproductively successful (Schuett et al. 2011). Therefore, parents that assort together with the highest levels of effort should be the most reproductively success. In this study, I determined how individuals expended their effort towards parental care and which cooperative strategy resulted in the highest reproductive success in Carolina Chickadees (*Poecile carolinensis*).

Carolina Chickadees are a good species to study the effects of parental cooperation on reproductive success. Carolina Chickadees are obligate cavity nesters and will readily use artificial cavities (Brewer 1961, Harrap and Quinn 1995), which allows for easy monitoring of parental behavior and reproductive activity. Chickadees exhibit biparental care where females are the sole nest builders, incubators, and brooders, but both parents contribute towards provisioning and nest defense (Brewer 1961). I focused my observations on the nestling stage where female brooding, provisioning, and nest defense behaviors are exhibited and cooperation is critical between shared tasks (Brewer 1961). I measured effort towards provisioning and nest defense in chickadees to determine how individuals approach parental care and I measured female brooding to look for evidence of persistency in parental effort since female brooding potentially conflicts with effort spent provisioning and defending the nest. I used similarity in parental effort between parents as a quantitative measurement of cooperation between parenting styles. To get a similarity measurement for each chickadee breeding pair, I created a similarity

index using the provisioning and nest defense z-scores. I determined if individual chickadees have parenting styles by measuring for consistency (i.e. repeatability of effort in provisioning and nest defense over time) and persistency (i.e. lack of compensation in effort towards provisioning during female brooding periods) in their effort towards parental care and I used the similarity index to determine how parenting styles of males and females may interact to best influence reproductive success.

METHODS

Study Species

Carolina Chickadees (*Poecile carolinensis*) are small passerine birds (9-12 g) native to the southeastern United States (Brewer 1961; Harrap and Quinn 1995; Mostrum et al. 2002). They are common across their range and inhabit mixed deciduous forests (Harrap and Quinn 1995; Mostrum et al. 2002). Carolina Chickadees are omnivorous; they primarily forage for arthropods, but rely more on seeds and other plant matter during the winter season (Mostrum et al. 2002). Carolina Chickadees are non-migratory and congregate in flocks during winter (Brewer 1961; Harrap and Quinn 1995; Mostrum et al. 2002). Dominant males establish nesting sites with females within the flock's territory before the breeding season begins (Brewer 1961; Harrap and Quinn 1995; Mostrum et al. 2002).

Carolina Chickadees are single-brood cavity nesters with nest building and egg laying taking place in the spring (Brewer 1961). Nests are constructed of moss (Andreas 2010) and nest construction begins approximately 20 days before the first egg is laid (Mostrum et al. 2002). A single egg is laid daily, typically in the morning, and the females initiate incubation after the last egg is laid (Mostrum et al. 2002). Clutch size ranges from 3-10 eggs. Incubation occurs for a period of 11-14 days and the chicks begin to fledge 16 days after hatching in late spring/early summer (Harrap and Quinn 1995). The fledglings remain near the nest and still rely on the parents for another 14-21 days before becoming fully independent (Harrap and Quinn 1995).

Study Site

Nest boxes were distributed along an altitudinal gradient (600 – 900 m) on or near the campus of Western Carolina University in the southern Appalachian Mountains of western North

Carolina in Jackson County (35.303387, -83.2267019). Boxes were located in a rural neighborhood, surrounded by mixed deciduous forests and on the campus of Western Carolina University campus. These sites were selected because there were established populations of Carolina chickadees and these sites were used in a previous study on this species (Britton and Ballentine 2019). I used a total of 42 nest boxes, which were donated by the Highlands Plateau Audubon Society. All boxes had the same dimensions (23 cm front height x 28.5 cm back height x 15 cm width x 15 cm depth x 2.5 cm depth) and were installed in the same way (fastened to 1.5 m sections of 1.27 cm aluminum conduit poles).

Data Collection

Starting at the end of February 2019, I checked every nest box once a week. When fresh moss was observed in a box, I increased the frequency of observations by two to three times a week to determine first egg date. Chickadees usually lay one egg a day in the morning until the clutch is complete (Mostrum et al. 2002), so if I found a nest with more than one egg, I back counted to determine the day the first egg was laid. I determined that the female initiated incubation via a touch test to see if the eggs were warm. The date of initiation for incubation was determined when the last egg was laid.

Mist Netting and Bird Banding

Since Carolina chickadees do not have obvious sexual dimorphism in their plumage (Harrap and Quinn 1995), I caught and color banded at least one parent at every nest box to distinguish between individuals within a breeding pair. Once the female started incubating, I used a single mist net (6 x 2.5 m) mounted on aluminum poles near each box. To lure the birds closer to the net and improve capture rates, I presented a taxidermic mount of an Eastern Screech Owl (*Megascops asio*) and played a combination of recorded Carolina Wren (*Thryothorus*

ludovicianus) and Tufted Titmouse (*Baeolophus bicolor*) alarm calls to initiate a defense response. I sexed individuals in hand by determining the presence or absence of a cloacal protuberance, which are found only on males during the breeding season, or by noting a brood patch, which are only found on females during incubation and brooding. I measured the weight, wing length, tail length, and tarsus length for each captured chickadee.

Measuring Provisioning and Female Brooding Behavior

I conducted two 8-hour observation sessions on day 5 (trial 1) and day 10 (trial 2) of the nestling stage. I mounted small video cameras (LawMate cameras; 3.5 cm length x 2 cm width x 0.5 cm height; Annandale, VA) on the outside base of the box facing up towards the cavity entrance. This camera position allowed for a clear view of the color bands so individual birds can be accurately identified with each visit to the nest. Since it was not always possible to tell if the parent carried food in the video footage and parental visits have already been shown to be an adequate estimate of food delivery (McCarty 2002), I used visits per hour per chick for each parent as my measure of provisioning effort.

Additionally, I calculated the percentage of time the females brooded during the first 8-hour observation period (trial 1) on day 5 of the nestling stage. A female was considered brooding when she spent more than 5 minutes inside the nest box.

Measuring Nest Defense Behavior

Since chickadees response more defensively towards small raptors (Gehlbach and Leverett 1995, Nolen and Lucas 2009), I assayed nest defense behaviors in the parents by presenting a taxidermic mount of an Eastern Screech Owl near the nest box (Mutzel et al. 2013b, Redmond et al. 2009). I used recorded Carolina Wren and Tufted Titmouse alarm calls to alert the parents to a potential threat and initiate a defense response. The trial began when at least one

parent arrived to defend the nest. Since Carolina Chickadees are known to partake in mobbing behaviors such as diving towards and hovering over predators (Gehlbach and Leverett 1995, Nolen and Lucas 2009) and there is a risk of mortality associated with getting close to a predator (Ghalambor and Martin 2001), I used distance (m) from predator as my measure of nest defense effort in individuals. I conducted two 7-minute trials where I recorded the distance (m) from the predator for each individual every 5 seconds. Individuals were identified during each trial by using binoculars to spot color bands. Trials where typically done on day 6 (trial 1) and day 8 (trial 2) of the nestling stage; however, additional trials were conducted, as needed, until I had two measurements of nest defense effort for each individual. No defense trials were performed on the same day as provisioning trials.

Measuring Reproductive Success (Fledge Success and Nestling Quality)

I measured the growth rate (grams per day) of the nestlings, the mass (g) of the nestlings before fledging, and the number of successful fledglings for each breeding pair of Carolina Chickadees. I weighed the nestlings with an electronic scale on day 2, day 5, day 8, day 10, and day 12 of the nestling stage. Day 12 weights were my measurement of fledgling mass (g). I measured fledging success by monitoring for the presence of nestlings after day 13. On day 13 of the nestling stage, I installed Thermochron iButtons inside the nest boxes to determine when all the nestlings fledged. The iButtons were set to record the temperature inside the nest boxes every five minutes. A drop in temperature inside the nest indicated that nestlings had fledged and left the box (Ballance 2018). I considered a temperature drop occurring during the day to reflect a successful fledge. I confirmed the iButton data accurately reflected fledging using video on 9 nest boxes. For other boxes, I set up camera traps to detect any evidence of predation. In one case, I detected a flying squirrel predation that occurred overnight. In no other cases did I detect

evidence of predation of nestlings with video or camera traps after day 16. Thus, I am confident that fledge success was accurate for nestlings that were at least 16 days old and from which other evidence (iButton, video camera, and camera traps) were consistent with fledging.

Similarity Index

I estimated similarity in parental effort between members of a pair to test my hypotheses on cooperation. If parental effort produced a trade-off between parental tasks, then parents should exhibit division-of-labor and parents should be dissimilar in provisioning and defense effort. If effort positively co-varied between behaviors, then parents should show similar levels of investment in tasks. I created a similarity index using z-scores for provisioning and defense. For each individual, I calculated the mean level of effort between trial 1 and trial 2 for both provisioning and nest defense. Then, I used individual means to compute the population-level mean and standard deviation (n = 40). I used the population-level mean and standard deviation to calculate z-scores ((value-mean)/SD) for defense and provisioning per individual. Because I measured nest defense as distance from predator, a closer response indicated a greater effort. Thus, I converted the defense scores by multiplying by -1 such that a high z-score would indicate high effort. I calculated the similarity score for defense and provisioning per breeding pair by subtraction (female z-score – male z-score). Scores further from zero indicate a greater difference in the amount of effort provided by the male and female within a pair. A more negative score indicates a greater contribution by the male within a breeding pair. Conversely, a more positive score represents a greater contribution by the female within a breeding pair. Similarity scores close to zero indicate more similar levels of effort between parents.

Statistical Analysis

I performed all statistical analyses in R version 3.5.2 (R Core Team 2016). I used a repeatability analysis to determine if the measurements of provisioning and nest defense within individuals were repeatable (Boake 1989, Bell et al. 2009). To determine if provisioning and nest defense were sex-based behaviors, I performed an F-test to check for equal or unequal variance followed by a two-sided t-test between males and females for both provisioning and nest defense. I used a simple linear model to examine how individuals divided up their effort towards provisioning and defense as well as to determine if individuals adjusted their effort towards provisioning based on a third parental task (i.e. female brooding) to see if compensation occurred within pairs. Any additional statistical tests were done using simple linear models unless otherwise stated. I performed all correlation analyses using the lm() function from base R.

To determine how similarity in effort impacted reproductive success, I performed a Multivariate Analysis of Variance (MANOVA) with the manova() function in base R. Supplementary analyses included examining the relationship between parent body condition and level of parental effort using data I collected from banded chickadees during the incubation stage. I created a body condition index (10,000 X mass/winglength^3) using methods from Senar et al. (1992) and determined if there were differences in male and female body condition via an F-test and two-sided t-test. I also examined the proportion of male effort towards total pair provisioning between parents to better understand the relationship between pair dynamics in effort and reproductive success. I used a Type II error rate of $\alpha = 0.05$ for all statistical tests.

Ethical Note

This study was conducted in accordance with the ethical standards for animal welfare of the Institutional Animal Care Committee at Western Carolina University IACUC No. AUP 2019-011.

RESULTS

Of the 42 available nest boxes, CACH built nests in 24 boxes during the 2019 breeding season. Of the 24 nest initiations, 20 were viable for data collection due to 5 abandonments (3 before incubation, 1 during incubation, and 1 after hatching) and 1 re-nesting event. Other species that used the boxes were (4) Eastern Bluebirds (*Sialia sialis*) and (2) Southern Flying Squirrels (*Glaucomys volans*). I banded a total of 16 males and 7 females, which resulted in 18 breeding pairs with one parent banded and 2 breeding pairs with both parents banded. The first Carolina Chickadee hatching occurred on May 2nd and the last hatching occurred on May 29th. The first fledging event occurred on May 19th and the last fledging event occurred on June 13th. Average clutch size was 5.3 nestlings and the average number of nestlings fledged was 4.5 fledglings. The average nestling stage length was 16.5 days. There were two confirmed predation events after day 13.

Repeatability of Parental Effort

The level of individual effort was repeatable for both provisioning ($\beta_1 = 0.85$, $r^2 = 0.53$, $n = 40$, $F_{1,38} = 42.4$, $p < 0.001$, Figure 1a) and nest defense ($\beta_1 = 0.67$, $r^2 = 0.73$, $n = 40$, $F_{1,38} = 103.2$, $p < 0.001$, Figure 1b). Further, males did not increase their provisioning rates when females spent more time brooding ($\beta_1 = 0.0089$, $r^2 = 0.037$, $n = 20$, $F_{1,18} = 0.69$, $p = 0.42$, Figure 2a) nor did females adjust their effort towards provisioning based on how much time she spent brooding ($\beta_1 = 0.0030$, $r^2 = 0.010$, $n = 20$, $F_{1,18} = 0.18$, $p = 0.67$, Figure 2b).

Allocation of Effort: Provisioning and Nest Defense

There was a positive correlation between provisioning and nest defense within individuals ($\beta_1 = 0.049$, $r^2 = 0.12$, $n = 40$, $F_{1,38} = 5.0$, $p = 0.031$, Figure 4) where parents who put

more effort into defense also provisioned more frequently. There was no evidence of sex-biased effort in provisioning (males: mean ± SD = 1.4 ± 0.16, females: mean ± SD = 1.0 ± 0.10, n = 40, t = -1.96, $df_{(unequal\ \sigma^2)}$ = 32.56, p = 0.059, Figure 3a) or nest defense (males: mean ± SD = 9.8 ± 1.1, females: mean ± SD = 8.6 ± 0.90, n = 40, t = -0.91, df = 38, p = 0.37, Figure 3b). Since I found no significant effect of sex on provisioning and nest defense effort, I did not account for sex in subsequent analysis of the effects of provisioning and nest defense on reproductive success.

Effects of Brood Size on Parental Effort

Brood size exhibited a non-significant positive effect on total pair provisioning (β_1 = 0.80, r^2 = 0.12, $F_{1,18}$ = 2.1, p = 0.16), but a significant negative effect on per nestling provisioning within pairs (β_1 = -0.36, r^2 = 0.35, $F_{1,18}$ = 9.7, p = 0.0061). So, there was a non-significant increase in total pair provisioning with increasing brood size, but per nestling provisioning decreased with increasing brood size. There was no significant relationship between brood size and nest defense intensity among individuals (β_1 = -0.85, r^2 = 0.092, $F_{1,38}$ = 3.8, p = 0.057).

Cooperation and Reproductive Success

The relationship between defense similarity scores and provisioning similarity scores exhibited four main patterns of cooperation among chickadee breeding pairs (Figure 5): overall higher male contribution where the male committed greater effort towards both provisioning and nest defense within the pair (n = 7), overall higher female contribution where the female committed greater effort towards both provisioning and nest defense within the pair (n = 2), division-of-labor where the male defended more and the female provisioned more within the pair

(n = 1), and division-of-labor where the male provisioned more and the female defended more within the pair (n = 10).

Since the provisioning and defense similarity scores were co-linear (Figure 6), I only used the provisioning similarity score in the one-way MANOVA because provisioning was the parental behavior directly affecting chick growth rate and fledgling weight. I did not include the number of successful fledglings in the model because there was no significant relationship between the number of successful fledglings and the provisioning z-score ($\beta_1 = 0.27$, $r^2 = 0.025$, $F_{1,18} = 0.47$, $p = 0.50$) or the defense z-score ($\beta_1 = -0.21$, $r^2 = 0.021$, $F_{1,18} = 0.39$, $p = 0.54$). Provisioning similarity between parents had a significant effect on chick quality measurements ($t_{Pillai} = 0.35$, $F_{2,17} = 4.5$, $p = 0.027$, Figure 6). However, there was no evidence to suggest that pairs were exhibiting positive assortative mating via provisioning effort ($\beta_1 = 0.23$, $r^2 = 0.023$, $F_{1,18} = 0.42$, $p = 0.53$) or nest defense effort ($\beta_1 = -0.11$, $r^2 = 0.0097$, $F_{1,18} = 0.18$, $p = 0.68$). Additionally, there were significant positive correlations in the proportion of male effort within total pair provisioning and average fledgling mass ($\beta_1 = 2.34$, $r^2 = 0.52$, $F_{1,18} = 19.3$, $p = 0.00035$, Figure 7a) as well as average chick growth per day ($\beta_1 = 0.21$, $r^2 = 0.35$, $F_{1,18} = 9.5$, $p = 0.0064$, Figure 7b).

Adult Body Condition

There was a significant difference in male (mean ± SD = 0.42 ± 0.01, n = 13) and female (mean ± SD = 0.53 ± 0.02, n = 6) body condition among banded chickadees caught during the incubation stage where females were in better condition than males ($t = 5.2$, $df = 17$, $p = 0.000067$). Males had negative non-significant trends in effort vs. body condition for both provisioning ($\beta_1 = -4.4$, $r^2 = 0.099$, $F_{1,11} = 1.1$, $p = 0.32$, Figure 8a) and nest defense ($\beta_1 = -36.1$, $r^2 = 0.096$, $F_{1,11} = 1.2$, $p = 0.30$, Figure 8b) whereas females had a positive non-significant trend

in provisioning effort vs. body condition ($\beta_1 = 6.2$, $r^2 = 0.46$, $F_{1,4} = 3.4$, $p = 0.14$, Figure 8a), but a positive significant relationship in nest defense effort vs. body condition ($\beta_1 = 39.6$, $r^2 = 0.87$, $F_{1,4} = 26.4$, $p = 0.0068$, Figure 8b).

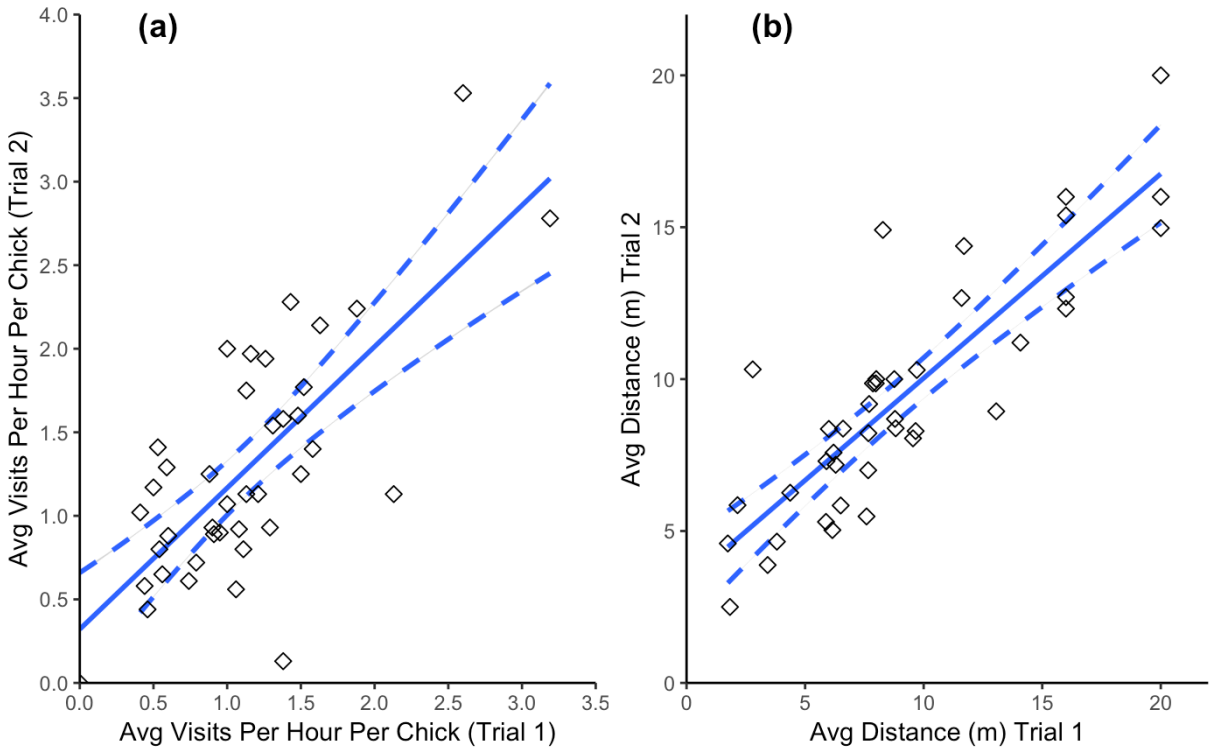

Figure 1. (a) Repeatability analysis ($\beta_1 = 0.85$, $r^2 = 0.53$, $F_{1,38} = 42.4$, $p < 0.001$) on provisioning behavior in individuals (n = 40) between trial 1 (average visits per hour per chick during an 8-hour observation period on day 5 of the nestling stage) and trial 2 (average visits per hour per chick during an 8-hour observation period on day 10 of the nestling stage). **(b)** Repeatability analysis ($\beta_1 = 0.67$, $r^2 = 0.73$, $F_{1,38} = 103.2$, $p < 0.001$) on nest defense behavior in individuals (n = 40) between trial 1 and trial 2 (average distance (m) from predator during a 7-minute observation period). The solid line represents the best-fit regression line and the dashed lines represent the 95% confidence bands.

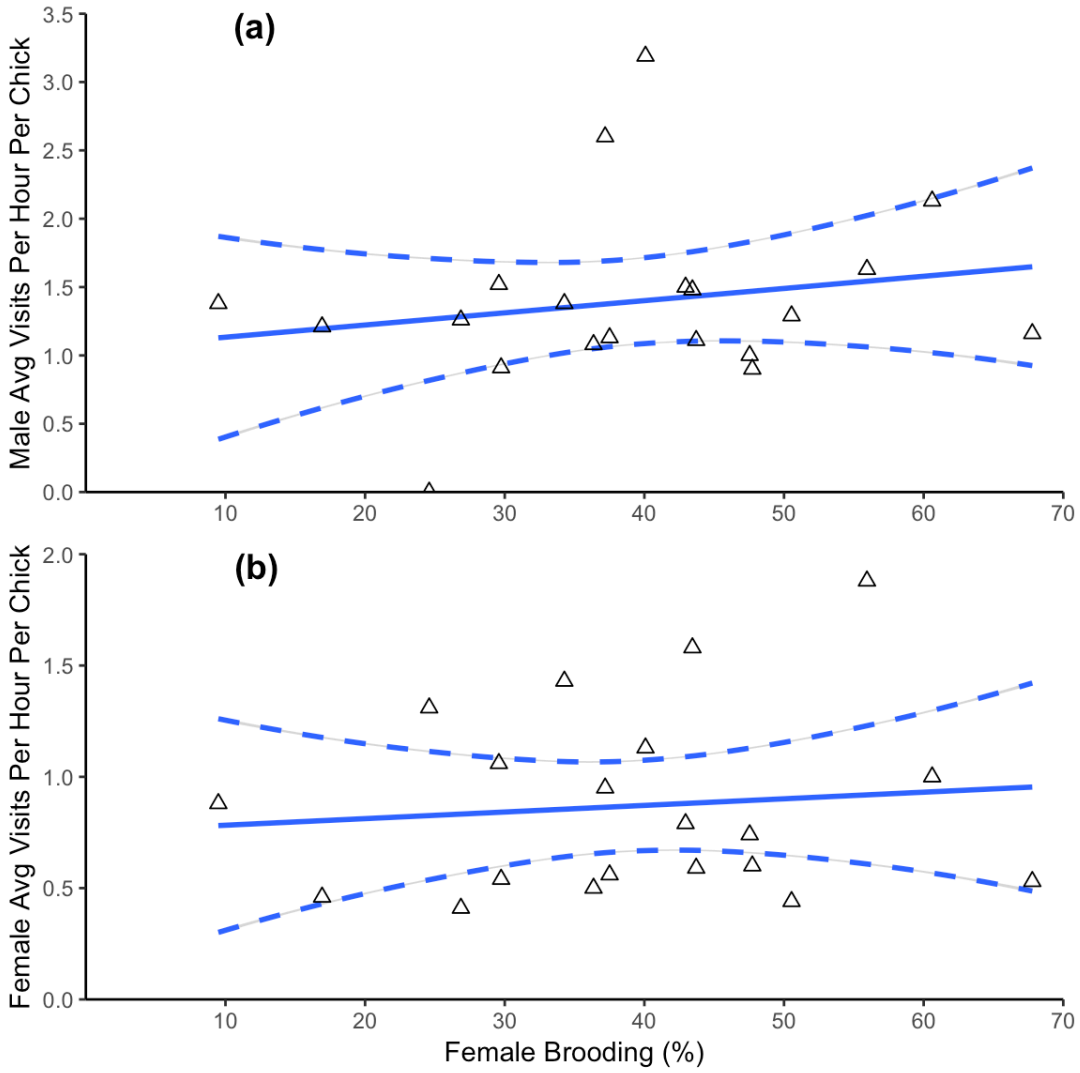

Figure 2. (a) Simple linear correlation analysis ($\beta_1 = 0.0089$, $r^2 = 0.037$, $F_{1,18} = 0.69$, $p = 0.42$) between percent female brooding over an 8-hour observation period on day 5 of the nestling stage and average male (n = 20) visits per hour per chick over an 8-hour observation period on day 5 of the nestling stage. **(b)** Simple linear correlation analysis ($\beta_1 = 0.0030$, $r^2 = 0.010$, $F_{1,18} = 0.18$, $p = 0.67$) between percent female brooding over an 8-hour observation period on day 5 of the nestling stage and average female (n = 20) visits per hour per chick over an 8-hour observation period on day 5 of the nestling stage. The solid line represents the best-fit regression line and the dashed lines represent the 95% confidence bands.

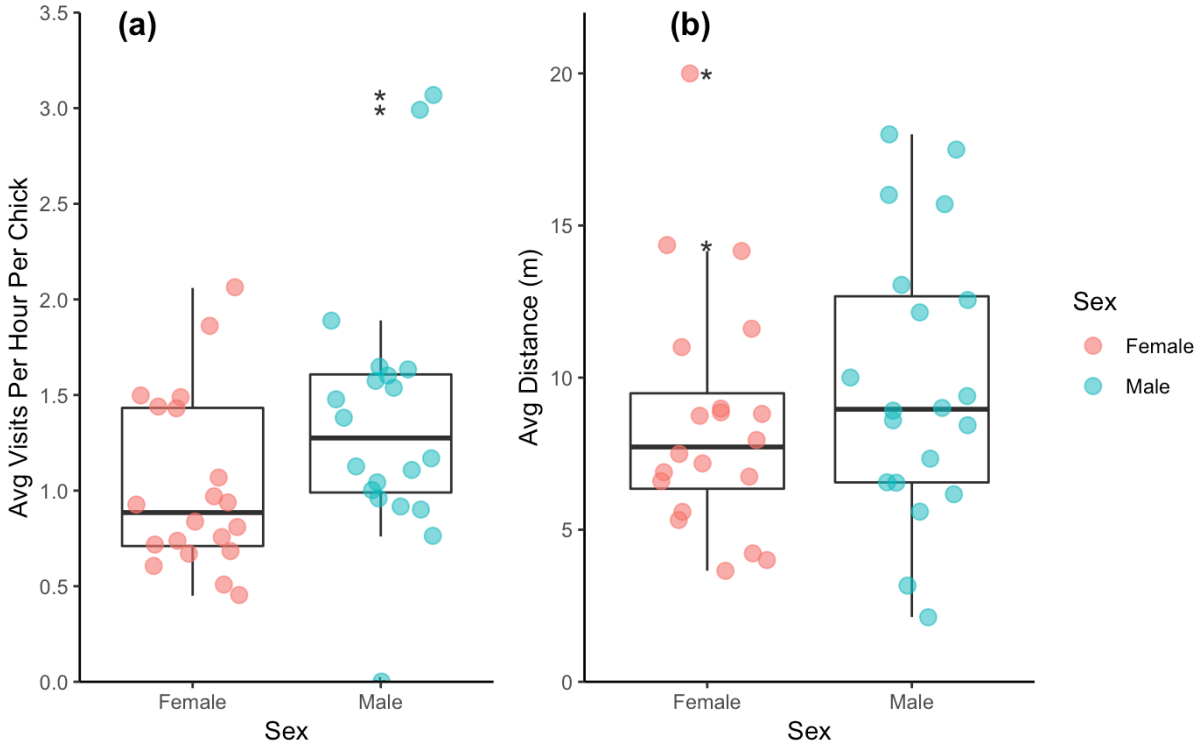

Figure 3. (a) Overall average visits per hour per chick (the average between provisioning trial 1 and trial 2 per individual) among males (1.4 ± 0.16, n = 20) and females (1.0 ± 0.10, n = 20). There was no difference in provisioning effort based on sex (t = -1.96, df = 32.56, p = 0.059). **(b)** Overall average distance (m) from predator (the average between nest defense trial 1 and trial 2 per individual) among males (9.8 ± 1.1, n = 20) and females (8.6 ± 0.90, n = 20). There was no difference in nest defense effort based on sex (t = -0.91, df = 38, p = 0.37). The box plots show the distribution of the data where the thick middle line represents the median, the box represents the interquartile range, the lower vertical line represents the data points below the 25th percentile, the upper vertical line represents the data points above the 75th percentile, and the asterisks are outliners.

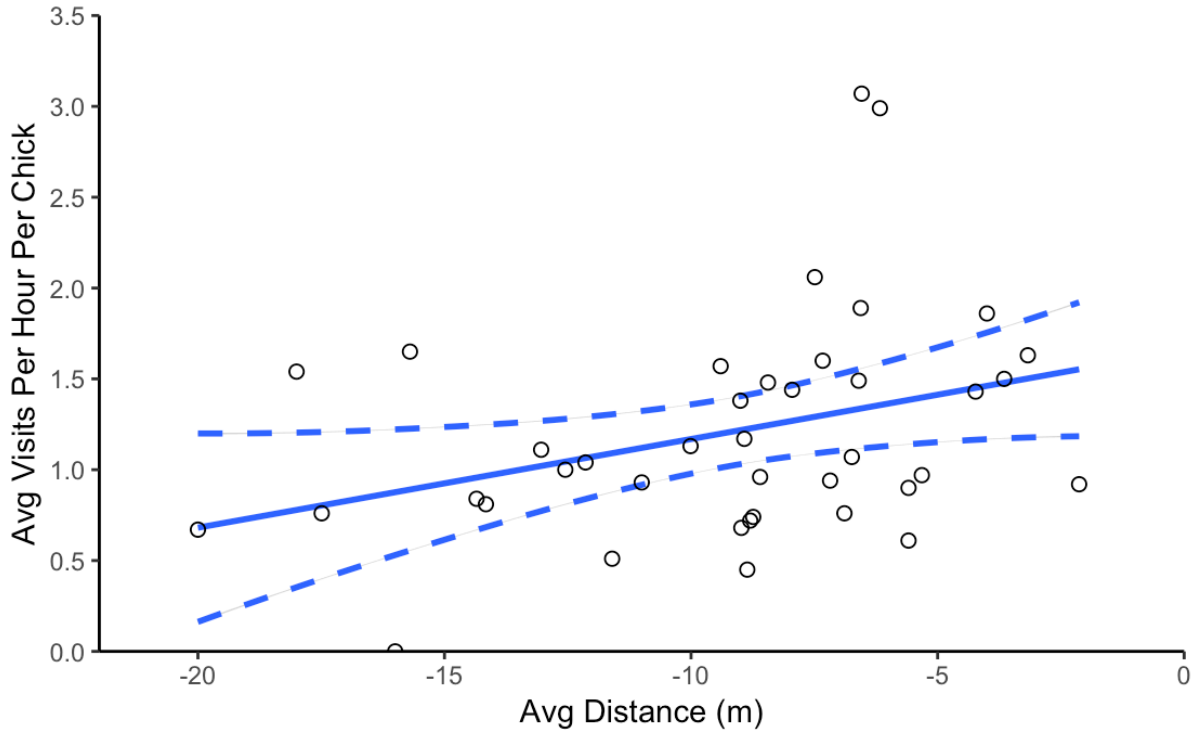

Figure 4. Simple linear correlation analysis ($\beta_1 = 0.049$, $r^2 = 0.12$, $F_{1,38} = 5.0$, $p = 0.031$) between individual ($n = 40$) contributions toward provisioning (average visits per hour per chick) and nest defense (average distance (m) from predator where a distance close to zero indicates high effort). Distance measurements were multiplied by -1 to adjust for the inverse relationship related to effort. The solid line represents the best-fit regression line and the dashed lines represent the 95% confidence bands.

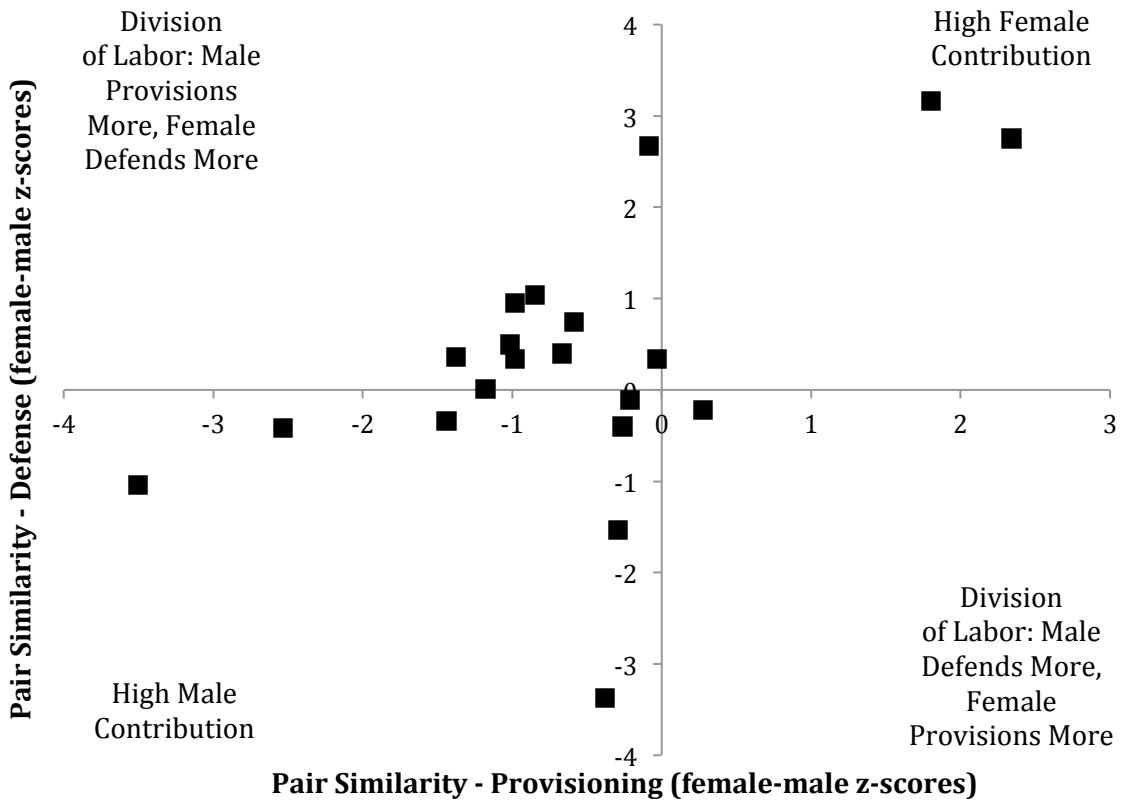

Figure 5. The relationship between provisioning similarity scores and defense similarity scores within breeding pairs (n = 20), which shows the variation in cooperation among breeding pairs. A negative score indicates greater male contribution towards the parental task within a pair and a positive score indicates greater female contribution towards the parental task within a pair. Points that are distributed closest to the origin indicate similar levels of effort in parental behavior between parents within pairs.

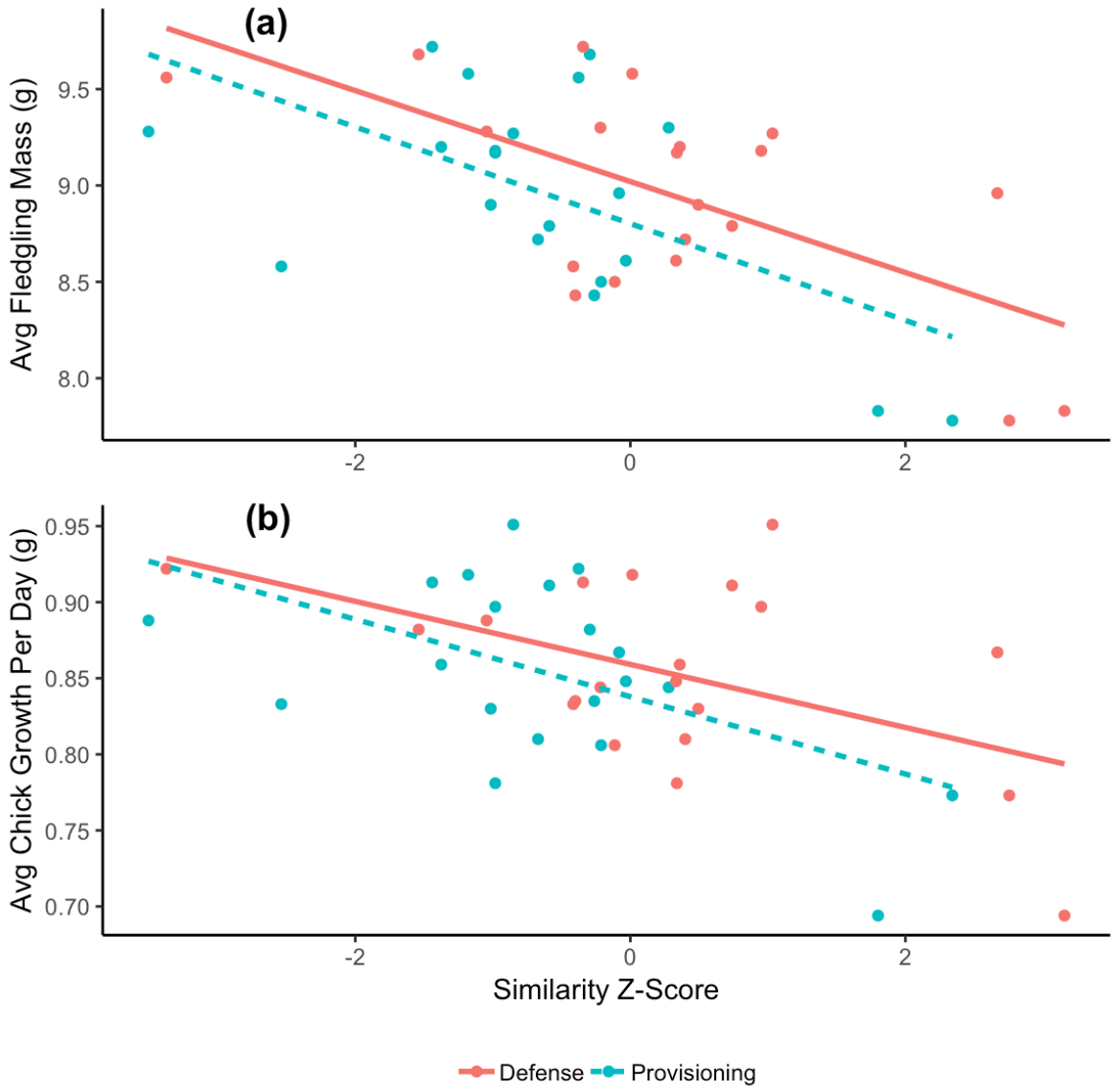

Figure 6. The relationship between similarity scores (level of similarity between male and female contribution within a breeding pair (n = 20)), **(a)** average fledgling mass (g), and **(b)** average chick growth per day (g). A score close to zero indicates high levels of similarity. A high negative score means low levels of similarity with the male being the higher contributor and a high positive score means low levels of similarity with the female being the higher contributor. Only the provisioning similarity z-score was used in the one-way MANOVA ($t_{Pillai} = 0.37$, $F_{2,17} = 4.5$, $p = 0.027$).

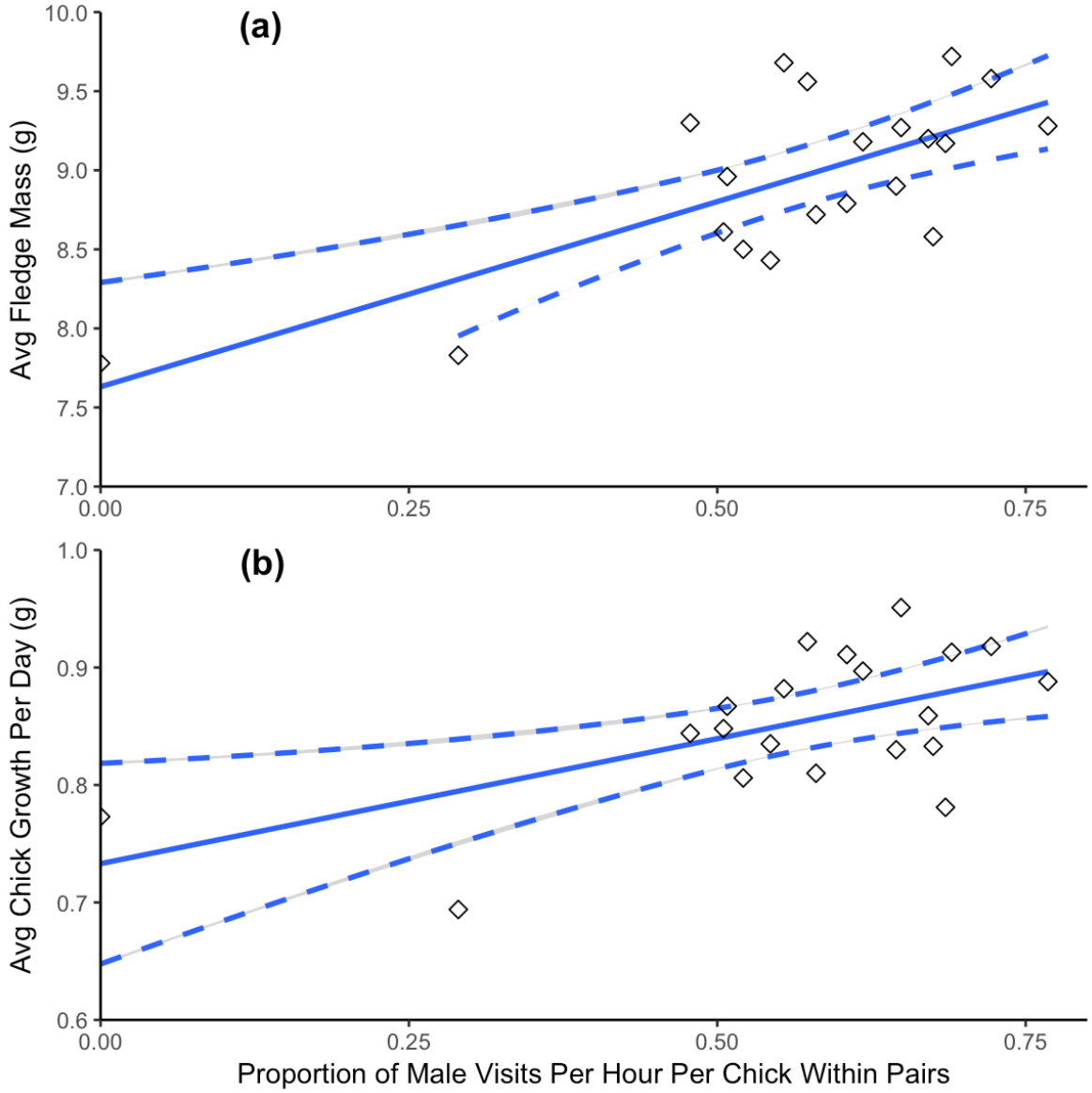

Figure 7. The proportion of male provisioning effort within total pair visitation rates per chick in relation to the **(a)** average fledgling mass ($\beta_1 = 2.34$, $r^2 = 0.52$, $F_{1,18} = 19.3$, $p = 0.00035$) and the **(b)** average chick growth per day ($\beta_1 = 0.21$, $r^2 = 0.35$, $F_{1,18} = 9.5$, $p = 0.0064$).

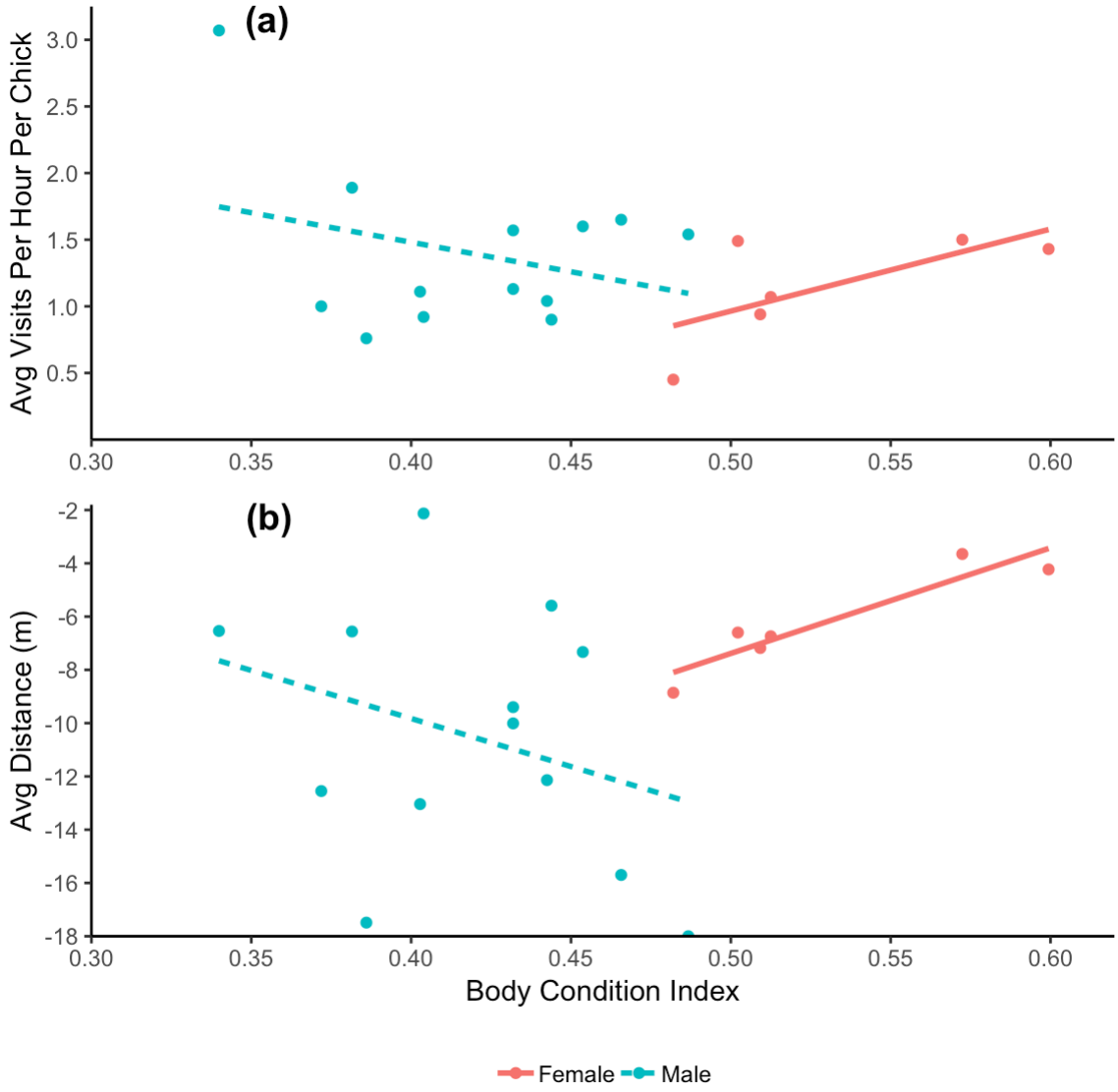

Figure 8. Body condition for male (n = 13) and female (n = 6) banded chickadees was determined using a body condition index (10,000 X mass/winglength^3). Females were in significantly better condition than males (t = 5.2, df = 17, p = 0.000067). Males exhibited negative non-significant trends in effort vs. body condition for both **(a)** provisioning (β_1 = -4.4, r^2 = 0.099, $F_{1,11}$ = 1.1, p = 0.32) and **(b)** nest defense (β_1 = -36.1, r^2 = 0.096, $F_{1,11}$ = 1.2, p = 0.30). Females exhibited **(a)** a positive non-significant trend in provisioning effort vs. body condition (β_1 = 6.2, r^2 = 0.46, $F_{1,4}$ = 3.4, p = 0.14), but **(b)** a positive significant relationship in nest defense effort vs. body condition (β_1 = 39.6, r^2 = 0.87, $F_{1,4}$ = 26.4, p = 0.0068). Distance measurements were multiplied by -1 to adjust for the inverse relationship related to effort.

DISCUSSION

In this study, I determined if individual Carolina Chickadees have parenting styles by measuring for consistency and persistency in their effort towards parental care and I used the similarity index to determine how parenting styles of males and females interacted to best influence reproductive success. Chickadee parents exhibited evidence of parenting styles by being consistent in their level of effort across time (Figure 1) and persistent in their level of effort across contexts or regardless of their partner's performance (Figure 2). Individuals exhibited parenting styles with positive correlations in effort between provisioning and nest defense where those who visited the nest more frequently also allocated more effort towards nest defense (Figure 4). Thus, parental contribution positively co-varied between multiple tasks, but parental performance varied from high to low, which could be driven by parent condition (Figure 8) or brood quality. Further, I found that when male effort matched or exceeded female effort, pairs produced high quality chicks (Figure 6, Figure 7). Therefore, the degree of parental contribution provided by the male chickadee in a pair impacts chick quality.

Parenting Styles

Parenting styles require parents to be consistent in their parental performance across time and persistent in their parental performance across context or regardless of their partner's performance (MacColl and Hatchwell 2003, Maestripieri 2001, Pittet et al. 2013, Wischhoff et al. 2018). Provisioning and defense behaviors in both males and females were repeatable across time within the same reproductive attempt (Figure 1). Thus, at least within a single breeding attempt male and female chickadees are consistent in parental effort, which agreed with other studies in that nestling stage and age of the nestlings did not alter parental effort (Knapton 1984,

Rauter et al. 2000). Further, in both male and female provisioning, female brooding did not significantly impact effort. During the brooding period when females are challenged by having to both provision and brood, neither male nor female provisioning rates changed in response to female effort. Females brooding 70% of the time provisioned at the same rate as females brooding 10% of the time (Figure 2b), so females did not decrease their provisioning effort with increasing brood percentage. In other species, brooding periods did not significantly interfere with female provisioning effort in Common Eiders (*Somateria mollissima*) (Mendenhall 1979) nor did increasing effort towards brooding appear to be a source of reproductive stress on female Pied Flycatchers (*Ficedula hypoleuca*) (Sanz and Moreno 1995). In this study, female brooding effort was likely influenced by environmental factors such as weather or ambient temperature within the nest cavity (Johnson and Best 1982). Thus, provisioning efforts by females were persistent.

If compensation occurred within pairs, I expected males to elevate their provisioning effort the longer females were engaged in brooding to compensate for the time the females were not provisioning the brood. Yet, male chickadees did not appear to react to the amount of time females spent brooding by increasing their provisioning rates on day 5 of the nestling stage (Figure 2a). Males with partners that engaged in brooding 10% of the time provisioned at the same rate as males with partners that engaged in brooding 70% of the time. Alternatively, the increase in male effort in provisioning during brooding periods could occur off the nest, which was not observable during the provisioning trials. Male chickadees are known to provision their partner when she is incubating or brooding (Brewer 1961), and while the females were brooding in this study, I observed males giving food to females at the nest on several occasions. However, all visits to the nest by the male was counted as provisioning because it was unknown whether

the female consumed the food or passed it to her brood due to the camera angle. Male visits to the nest were still persistent during female brooding periods because there was no observed compensation in male effort with increased brooding by the female. Finding that Carolina Chickadees are consistent in provisioning and defense as well as persistent in provisioning supports the hypothesis that they have parenting styles.

Since chickadees do display some evidence of having parenting styles, I predicted that individual effort allocation would positively co-vary or exhibit trade-offs. In this study, individuals exhibited parenting styles with positive correlations in effort between provisioning and nest defense (Figure 4). Thus, parent contribution positively co-varied between multiple tasks, but parental performance varied from high to low. Similar patterns of task allocation between different parental behaviors were documented in individual House Sparrows (Kopisch et al. 2005, Wetzel and Westneat 2014), Willow Tits (*Poecile montanus*) (Rytkönen et al. 1995), and Stonechats (*Saxicola torquata*) (Greig-Smith 1980). Additionally, there was no sex-bias differences in parenting styles between male and female chickadees for both provisioning and nest defense (Figure 3), which coincides with other studies (Nealen and Breitwisch 1997, Neudorf et al. 2013). Even though provisioning and nest defense are shared tasks, one sex will not always commit to higher levels of effort over the other in chickadees as seen in other species (Fraser et al. 2002, Port and Greeney 2015). Since chickadees exhibited positive correlations in effort between provisioning and nest defense, possible factors that could influence parental performance are parent condition or the reproductive value of the brood.

The Effect of Parent Condition on Parental Performance

Good quality parents maintain higher levels of effort across multiple tasks over low quality parents. One intrinsic driver of parent quality could be body condition. Individuals in

better condition will have greater fat storage in the body (Johnson et al. 1985). These energy reserves can support higher levels of effort towards parental care. Body condition in Common Terns (*Sterna hirundo*) was found to be highly stable in individuals, but varied greatly between individuals (Wendeln and Becker 1999). Body condition in terns was also positively correlated with effort, which resulted in higher reproductive success (Wendeln and Becker 1999). Also, parents in better condition delivered larger meals to chicks in Antarctic petrels (*Thalassoica antarctica*) (Tveraa et al. 1998). For the banded chickadees in this study, females were generally in better condition than the males, and there were positive trends between body condition and effort for both provisioning and nest defense for banded female chickadees (Figure 8).

Banded male chickadees, on the other hand, showed negative non-significant trends between body condition and effort for both provisioning and nest defense (Figure 8). This trend could be evidence of males compensating for their poor physical condition by being better parents to maintain their attractiveness to their partner as predicted by the differential-allocation hypothesis (Burley 1986). This relationship was also evident in Northern Cardinals (*Cardinalis cardinalis*) where males with duller plumages, and thus of poorer condition, were better parents over brighter males in better condition (Jawor and Breitwisch 2004). Alternatively, males in worse condition will have lower survival rates (Benson and Bednarz 2010) and have reduced chances of future reproductive opportunities. So, males in worse condition may instead be allocating more effort towards the current brood to maximize the success of their last potential reproductive attempt. Another possible explanation for this negative trend is that males in better condition are adopting mixed reproductive strategies and engaging in extra-pair copulations. Extra-pair copulation is a phenomenon exhibited in many bird species that use biparental care where individuals form breeding pairs (i.e. social mates), but still seek outside reproductive

opportunities (Otter et al. 1998, Reudink et al. 2006). No studies have directly measured extra-pair copulation rates in Carolina Chickadees (Reudink et al. 2006), but for a close relative, the Black-capped Chickadee (*Poecile atricapillus*), extra pair offspring accounted for approximately 15% of total offspring, but were present in approximately 30% of the nests (Mennill et al. 2004). Males maximize their reproductive success by optimizing the quantity of offspring sired and benefit through extra-pair copulations by siring offspring they do not have to care for (Trivers 1972). Male chickadees in better condition may have more opportunities for extra-pair copulations because females may be more likely to engage in extra-pair copulations with males in better condition especially if she is paired with a partner in poor condition (Mennill et al. 2004, Trivers 1972). Thus, males in better condition may not be as invested in caring for the current brood with their social mate if they were successful in copulating with neighboring females.

Another potential intrinsic driver of parent performance unrelated to physical condition is individual temperament or 'animal personality'. Currently, there are five classes of personality traits: activity, aggressiveness, boldness, exploration, and sociability (Réale et al. 2007). Certain personality traits have been shown to affect the expenditure of effort towards different parental tasks in birds such as aggression and exploration influencing provisioning rates (Mutzel et al. 2013a), and boldness influencing effort towards nest defense (Wischhoff et al. 2018). Personality traits may also influence behavioral syndromes, which are suites of correlated behaviors (Sih et al. 2004). In the case of this study where effort towards provisioning and nest defense are positively correlated in chickadees, a behavioral trait, such as aggressiveness, could be influencing the correlation where more aggressive individuals are more capable of defending the nest and provisioning more frequently. A similar relationship may be evident in Great Tits

(*Parus major*) based on the exploration trait in individuals (Both et al. 2005). While 'animal personality' seems to be an ideal candidate for producing parenting styles in chickadees, it is difficult to isolate personality traits as the cause from other potential avenues of consistent between-individual differences in parental performance, such as body condition in the context of this study. Many personality studies in relation to parental care in birds measure repeatability of parental behaviors between broods or across seasons (Both et al. 2005, Mutzel et al. 2013a, Wischhoff et al. 2018). Carolina Chickadees are single-brooded, so in this study, I measured repeatability within one breeding season; therefore, future studies will require multiple breeding seasons to determine if personality is fueling the consistent variation in parental performance in chickadees.

Extrinsic factors such as habitat quality, prey abundance, and weather can also affect parental performance (Dawson and Bortolotti 2000, Ens et al. 1992, Hakkarainen et al. 1997). In this study, there was no significant variation in habitat other than elevation. The nest boxes were randomly place within a 600-900 m elevational range in mixed deciduous forest in the Southern Appalachian Mountains. There was no significant difference in chickadee parental performance based on elevation. Weather was also relatively stable throughout the breeding season with only one or two weekends with severe weather conditions (i.e. heavy rain and thunderstorms). However, overwintering conditions could have a significant impact on body condition in non-migratory species (Montreuil-Spencer et al. 2019), which could later influence parental performance during the breeding season in chickadees. Prey abundance was not measured for this study.

The Effect of Brood Value on Parental Performance

Parental investment theory provides a potential explanation for the positive correlations in effort between provisioning and nest defense as seen in chickadees (Griggio et al. 2009, Redmond et al. 2009, Rytkönen 2002). Parental investment (PI) theory predicts that parents should invest more in larger rather than smaller broods and higher rather than lower quality offspring (Carlisle 1985, Montgomerie and Weatherhead 1988, Trivers 1972). Multiple studies have shown that brood size creates a positive effect on provisioning rates in birds (e.g. Biermann and Sealy 1982, Johnson and Best 1982) including Carolina Chickadees (Britton and Ballentine 2019). In this study, parents displayed a non-significant positive trend in total pair provisioning in relation to brood size, but a significant negative relationship between per nestling provisioning and brood size. My findings align with Lack's principle where brood size is regulated by the number of offspring parents can successfully feed (Lack 1954) and Trivers' theory of parental investment where the more offspring there are the less the parents can invest in each (Trivers 1972). Additionally, PI theory predicts that parents who have invested in a larger brood may be more willing to take on risks and defend the nest more vigorously. Female Merlins (*Falco columbarius*), for example, have been documented to increase or decrease nest defense intensity based on respective increases and decreases in brood size manipulations (Wiklund 1990). In my study, however, there was no significant relationship between brood size and the willingness for chickadee parents to get close to predators when defending the nest, which was also found in Tree Swallows (*Tachycineta bicolor*) in regards to chasing off intruders (Lombardo 1991). Therefore, brood size may provide a partial explanation for variation in parental performance in provisioning, but not nest defense for the Carolina Chickadee.

According to the parental investment (PI) theory, the quality of the brood should also influence parental performance and create positive correlations in effort between provisioning and nest defense among parents. Chick quality can affect the reproductive value of the brood because good quality chicks are more likely to survive after fledging over low quality chicks (Monro´s et al. 2002, Naef-Daenzer et al. 2001); therefore, parents should provision good quality chicks more frequently (Griggio et al. 2009) and risk themselves more in defending a nest full of reproductively valuable offspring (Montgomerie and Weatherhead 1988). For example, parents increased their nest defense intensity when brood quality was experimentally manipulated via supplemental feedings in Great Tits (*Parus major*) (Rytkönen 2002). Additionally, there are honest signals of chick quality such as feather ornamentation as exhibited in Rock Sparrow chicks (*Petronia petronia*) (Griggio et al. 2009) or moth color components as exhibited in European Starling (*Sturnus vulgaris*) (Jacob and Heeb 2013) and Barn Swallow chicks (*Hirundo rustica*) (de Ayala et al. 2007). In this study, provisioning effort and chick quality were correlated (Figure 6), but it is impossible to determine if the quality of the brood resulted in better parental performance or if the quality of the brood was a result of care provided by better quality parents in the context of this study.

Male-Female Dynamic and Reproductive Success

Parenting styles should dictate optimal strategies to maximize reproductive success. If individuals exhibit parenting styles with positive correlations in effort between behaviors, then I predicted that parents would assort by similarity and parents with the highest levels of effort should have the highest reproductive success. While multiple species have displayed positive assortative mating via behavioral traits (Both et al. 2005, Harris and Siefferman 2014, Nealen and Breitwisch 1997, Schuett et al. 2011, Spoon et al. 2006), chickadees do not appear to follow

that pattern of pairing with only four pairs within the study population showing a high level of similarity in both provisioning and nest defense effort (Figure 5). Surprisingly, even though the study population exhibited a positive correlation in effort between provisioning and nest defense among individuals, division-of-labor was the most common strategy where 50% of the pairs had the male provision more and the female defend more (Figure 5). Chickadees are not the only species that favor division-of-labor among shared tasks. The division-of-labor strategy is also expressed in House Sparrows (Bartlett et al. 2005), Tree Swallows (Lombardo 1991), and Northern Mockingbirds (*Mimus polyglottos*) (Zaias and Breitwisch 1989). Additionally, 35% of chickadee pairs within the study population had overall higher male contribution, which is also exhibited in black-billed magpies (*Pica hudsonia*) (Buitron 1988). In this study, the primary driver of reproductive success was the contribution of male provisioning in pairs.

There was no relationship between parental cooperation and number of nestlings fledged, but the growth rate and the mass of the nestlings on day 12 of the nestling stage were affected by the interaction between male and female parenting styles. Any pair where the male exceeded the provisioning effort of the female or at least matched her in effort produced good quality chicks, so pairs with highly similar parenting styles or dissimilar parenting styles with the male being the higher contributor were the most reproductively successful (Figure 6). Additionally, the greater the proportion of male effort towards provisioning per chick within pairs equated to increasingly higher growth rates and higher fledgling weight (Figure 7). The direct relationship between male provisioning effort and brood quality was also found in Black-throated Blue Warblers (*Dendroica caerulescens*) (Stodola et al. 2010). Furthermore, there was no significant relationship between total pair provisioning (male + female effort) and growth rate or fledgling mass in Carolina Chickadees, which also coincides with the findings of Stodola et al. (2010).

Thus, only male contribution towards provisioning mattered in the cooperative system of the Carolina Chickadee.

There are two main implications regarding male provisioning performance dictating brood quality. First, male provisioning performance dictating brood quality suggests a larger scale division-of-labor within the reproductive attempt. Chickadee females are known to invest heavily in pre-nestling and early nestling duties (Brewer 1961), so it is up to the male to contribute more towards later stage parental tasks, such as provisioning of the nestlings, to ensure the quality of the brood. This same dynamic is also apparent in the Black-throated Blue Warbler (Stodola et al. 2009). Large scale division-of-labor benefits each parent within the biparental system by allocating the burden of care towards offspring temporally. Thus, if males carry the burden of provisioning the brood for later in the reproductive attempt, then females can focus their effort more on nest building, eggs, incubation, and brooding to ensure the quantity of the brood. Second, the life-history trade-off between parental effort and parental survival differs between the sexes (Santos and Nakagawa 2012). Males lose more weight (Royle et al. 2002) and are less likely to survive (Santos and Nakagawa 2012) when they increase their effort towards shared tasks. Female birds, on the other hand, are just as likely to survive even with increased parental effort (Santos and Nakagawa 2012). So, males are more likely to lose future reproductive opportunities the more they invest heavily in the current brood. Given the cost, they must be sure of the value (Mock et al. 2005) and paternity of the brood (Dixon et al. 1994, Sheldon and Ellegren 1998). Male surety in paternity of the brood could explain the greater variation in provisioning and nest defense effort among male chickadees compared to female chickadees in this study (Figure 3). As discussed above, male body condition may play a role in parental performance (Figure 8). Males in poor condition may increase their effort due to

reduced chances of survival to the next reproductive opportunity. Males in good condition may be engaging in extra-pair copulations and reserving their energy to increase survival for future breeding opportunities.

This study provides an in depth examination of the dynamic between male and female parenting styles. Male chickadees must be the dominant contributor towards provisioning within the pair to produce larger, better quality chicks at fledging. Chick quality can affect the reproductive success of the pair because good quality chicks are more likely to survive after fledging. Female investment towards female-only tasks in the early stages of the reproductive attempt dictates the quantity of the brood. Within the biparental system of the Carolina Chickadee, this dynamic between males and females within pairs allows for maximal reproductive success.

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